Sedimentary habitats and molluscan faunas of Bahia la Choya (Gulf of California, Sonora, Mexico)

By

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With 13 figures in the text and 10 plates

ABSTRACT

The tidal flat complex of Bahia la Choya can be subdivided into fine- to medium-sandy outer flat areas characterised by sand waves, a fine-sandy rippled mid flat, and a fine-sandy to silty inner flat with a mesita-like topography. Additional habitats are a major tidal channel, a supratidal salt marsh, and a shelly spit separating the marsh from the tidal flat. Lithified Pleistocene rocks crop out at various localities, especially in the northern part of the bay. Biogenic sedimentary structures are ubiquitous on the tidal flat and include feeding excavations of rays, crawling traces of gastropods and hermit crabs, shafts of polychaetes, and burrows of crabs and callianassid shrimps. A zonation of biogenic sedimentary structures allows differentiation of the outer/mid flat and the inner flat/salt marsh. The shelly benthic macroinvertebrate fauna belongs to the Panamic faunal province and is dominated by molluscs, among them 127 species of bivalves, 88 of gastropods, and three of scaphopods. Highest shell densities occur in outermost intertidal areas, low densities are characteristic of inner flat firmgrounds. In death assemblages bivalves dominate numerically except in inner flat areas and in the channel; they are also less dominant in hard substrate areas where they constitute 40—70% of the fauna. Highest diversity values of the thanatocoenoses are found in outer to mid flat areas, whilst lowest values are encountered in the inner flat of the southern part of the bay. These general distribution patterns suggest that the distribution of species within death assemblages across the tidal flat is largely governed by ecologic factors and less by taphonomic processes such as post mortem transport.

KURZFASSUNG

Das Watt von Bahia la Choya läßt sich in drei Abschnitte unterteilen: Ein fein- bis mittelkörniges äußeres Sandwatt mit Großrippeln, ein feinkörniges flaches Mittelwatt mit Kleinrippeln und ein feinsandig bis siltiges Innenwatt mit einer „Tafelberg"-Morphologie. Landwärts trennt eine Schillbarre die Salzmarsch von der Gezeitenfläche. Sowohl Salzmarsch wie Watt werden von einer größeren Gezeitenrinne durchzogen. Lithifizierte Sedimente des Pleistozäns finden sich in der Umrandung der Bucht und vor allem im nördlichen Teil der Gezeitenfläche. Lebensspuren sind im gesamten Wattbereich sehr häufig. Es handelt sich um schüsselförmige Depressionen, die von Rochen erzeugt wurden, um Kriechspuren von Gastropoden und Einsiedlerkrebsen, um agglutinierte Wohnröhren von Polychaeten und um Wohnbauten von Krabben, *Callianassa* und *Upogebia*. Die Zonierung der Spuren erlaubt eine Unterscheidung des äußeren und mittleren Watts vom Innenwatt und der Salzmarsch. Das hartteiltragende Makroinvertebraten-Benthos gehört der Panama-Faunenprovinz an und besteht vorwiegend aus Mollusken. 127 Muschelarten, 88 Gastropodenarten und 3 Scaphopodenarten wurden identifiziert. Die größte Schalendichte findet sich im äußersten Intertidalbereich; die Festgründe des Innenwatts besitzen hingegen nur eine geringe Schalendichte. In den Thanatozönosen dominieren die Muscheln zahlenmäßig bei weitem; lediglich im Innenwatt und in der Gezeitenrinne sind Gastropoden häufiger. Auf Hartsubstrat stellen Muscheln 40—70% der Fauna. Die höchsten Diversitätswerte der Thanatozönosen treten im Außen- und Mittelwatt auf; die geringsten Werte weist das Innenwatt im südlichen Bereich der Bucht auf. Diese allgemeinen Verteilungsmuster deuten an, daß die Verteilung von Arten in den Thanatozönosen des Watts vorwiegend von ökologischen Faktoren bestimmt wird und nicht so sehr von taphonomischen Prozessen wie postmortaler Transport.

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INTRODUCTION

Bahia la Choya, a small protected bay in the northern part of the Gulf of California, is a natural laboratory for the study of taphonomic processes and paleoenvironmental indicators. The rich molluscan fauna, the low sedimentation rates and the broad intertidal zonation make the area ideally suited for actualistic studies. Nearby fossiliferous deposits of Pleistocene age provide the opportunity to evaluate the utility of such actualistic studies for paleoenvironmental purposes. Thus, our studies have two purposes: (1) Analysis of the nature and distribution of potential paleoenvironmental indicators in the

Recent habitats of Bahia la Choya. We consider biotic, taphonomic, sedimentologic, and ichnologic environmental indicators. (2) Application and evaluation of these paleoenvironmental indicators in an analysis of adjacent fossiliferous deposits of Pleistocene age. We demonstrate how an integrated approach to paleoenvironmental analysis is an especially powerful technique in paleoecology.

A summary of our work is presented in Fürsich & Flessa (1987) and a field guide to the region is available (Flessa 1987).

THE REGIONAL SETTING

Bahia la Choya is located at approximately 31°21′ north latitude, 113°37′ west longitude, on the northeastern shore of the Gulf of California (Fig. 1), in the Mexican state of Sonora. The Bahia la Choya area is shown on the 1981 Puerto Peñasco 1:50,000 topographic sheet (Map code H12A32) published by the Comision de Estudios del Territoria Nacional, Direccion de Estudios Economicos, Mexico City. Puerto Peñasco, a town of approximately 40,000 inhabitants (in 1988), is 10 km to the southeast of Bahia la Choya.

We use Mexican place names throughout. Because of the area's proximity to the United States (100 km from the border

at Lukeville, Arizona) and the influx of American tourists, English-language place names are often used in the region. Bahia la Choya is "Cholla Bay" and Puerto Peñasco is "Rocky Point" [the literal translation is "Rocky Port"] to most Americans.

The region is within the Sonoran Desert. The climate is arid, with an annual average rainfall of 74 mm (Thomson et al. 1969). The rainfall is seasonal: part falls during brief but often violent summer thunderstorms, the remainder falls during the winter as the remnants of Pacific Ocean storms move across the area. Tropical storms and hurricanes occasionally affect

Fig. 1: Oblique aerial photograph of Bahia la Choya. M: salt marsh; IF: inner flat; MF: mid flat; OF: outer flat; ST: subtidal; C: channel.

the region in the late fall. Evaporation greatly exceeds precipitation and vegetation is limited to sparse cactus and desert shrubs and grasses.

All streams in the immediate region are ephemeral. The "esteros" of the area are negative estuaries, where evaporation significantly exceeds runoff. The only perennial stream entering the northern Gulf of California is the Colorado River, 120 km to the northwest. The influx of both fresh water and sediment from the Colorado River is limited. Dams and irrigation projects have reduced river flow in the delta region to such low levels that evaporation eliminates the remaining fresh water during most of the year.

Daily average air temperatures range from 11.6° C in January to 30° C in August (THOMSON 1987). Summer extremes of 42° C and winter extremes of 0° C are not uncommon in this harsh climate.

Surface water temperatures range from 10°–14° C in the winter to 30°–32° in the summer. Salinity in the Gulf of California ranges from 35‰ in offshore surface waters to 39‰ in shallow coastal waters. Higher salinities occur in the upper reaches of esteros and in evaporite basins along the margins of Bahia Adair.

The tidal range in the northern Gulf of California is the third highest in North America. Spring tides in the Puerto Peñasco area often reach 8 to 9 m of vertical displacement. Tides are of the mixed, semidiurnal type: two unequal high and two unequal low tides occur each day. The very low slope of the intertidal area and the very great tidal range result in an extensive area of exposure during spring low tides. Approximately 10 km² of tidal flats are exposed during exceptionally low tides. The large tidal range also produces strong currents in the channels that drain the marsh and the sand flats. We have observed current velocities of 1 m/sec in tidal channels.

The fauna of the Gulf of California is included within the Panamic Province, a largely tropical biogeographic province that ranges southward to Panama. The fauna of the northern Gulf has more in common with the truly tropical faunas to the south than it does with the faunas on the Pacific coast of Baja California. BRUSCA (1980) provides a guide to the common intertidal invertebrates of the Gulf. KEEN (1971) is the authoritative reference to the Gulf's molluscs, and BECKVAR et al. (1987) present a key to the most common molluscs of the Bahia la Choya area.

GEOLOGIC SETTING

The Gulf of California is a rift basin which began opening approximately four million years ago (LARSEN et al. 1968; MOORE & CURRAY 1982). At its southern opening, the Gulf's rift system connects with the East Pacific Rise at a triple junction. Within the Gulf, the rift system consists of a series of short spreading zones offset by transform faults. At the northern end of the Gulf, this system connects, via transform faults, with the San Andreas fault system in southern California (ANDERSON 1971). The rift system marks the boundary of the North American Plate (to the east) and the Pacific Plate (to the west).

The Pinacate Mountains, an extensive complex of Plio-Pleistocene volcanoes lie to the north of the Bahia la Choya region.

Igneous rocks crop out on the northern and southern edges of Bahia la Choya. To the north, Cerro Prieto is a 125 m high hill of basaltic composition. The rocks are vesicular, olivine basalts. Lithologically similar rocks at Puerto Peñasco yielded a K – Ar date of 15 million years (LYNCH 1981). The southern margin of Bahia la Choya is defined by the 150 m high headland of Punta Pelicano. The headland consists of coarsely

crystalline granite, composed primarily of quartz and microcline. No radiometric dates have been reported, but it probably pre-dates the basaltic rocks of Cerro Prieto and Puerto Peñasco.

Sedimentary rocks in the region include poorly to well-consolidated sandstones of Pleistocene age. Poorly cemented alluvial fan and aeolian deposits occur at higher elevations and richly fossiliferous outcrops of shallow marine sandstone and conglomerate line the margins of Bahia la Choya and crop out in the northern portions of the bay's intertidal zone. These marine deposits (termed "beachrock" by EKDALE [1987]) consist of locally-derived rock fragments, coarse, angular grains of quartz and feldspar, and whole and fragmented molluscan shells. Cements consist of both aragonite and calcite.

No radiocarbon ages of these sedimentary deposits are available. JONES (1975) reports them as beyond the effective range of the technique. The faunal composition and relative elevation of the marine deposits lead HERTLEIN & EMERSON (1956) and ORTLIEB (1981) to assign a late Pleistocene age to the deposits.

SAMPLING METHODS

Between December 1985 and April 1986 we collected 77 samples from four transects (A through D of Figure 3) across the tidal flats. The transects extend from the shallow subtidal to the supratidal of the beach. Transects vary from 1600 m to 2100 m in length. Samples were taken and observations were

made at 100 m intervals along each transect. At each sample locality we collected 9 liters of sediment from the upper 5 cm of the tidal flats. Where shell density was low, we collected twice this amount and then normalized abundances to our standard 9 liter sample size. Sediment was wet-sieved in the

field, using a screen with a mesh size of 3 mm. The remaining sediment and shells were brought to the laboratory, where live and dead individuals were separated, identified, and counted. We also identified and counted all the live shelly macrofauna in the sample area and noted any surficial sedimentary structures. Additional samples were collected for analyses of grain size distribution and carbonate content. Observa-

tions on biofabric and burrows were made using shallow (20 cm) trenches or with box cores.

Twelve additional samples were taken along subtidal extensions of the transects. Water depths at low tide ranged from 2 m to 7 m. Samples were collected with a Petersen Grab or by SCUBA divers.

ENVIRONMENTS OF BAHIA LA CHOYA

The Bahia la Choya tidal flat complex exhibits a zonation readily recognised by the topography and vegetation (Figs 1, 2). The tidal flat can be subdivided into outer flat areas characterized by sand waves, a mid flat with a more or less flat rippled surface and an inner flat with a mesita-like topography. Each of these zones is characterized by a number of sedimentary and biotic features which are discussed below. Additional habitats are: a major tidal channel which crosses the tidal flat complex; the supratidal salt marsh complex; and the shelly spit between the marsh and tidal flat complex. The vegetation of the marsh consist of *Salicornia, Sueda,* and *Distichlis.* Small patches of marsh also exist on the seaward side of the spit. Where the tidal channel cuts through the spit an

ebb tidal delta is developed. It consists of tidal flat sands with a high admixture of shells and shell debris washed out from the spit. On the mid flat, some distance north of the channel, an elongated sand bar running more or less parallel to the channel (and nearly normal to the beach) is developed. It consists nearly exclusively of shell debris and appears to be stationary except during strong storms when it migrates landward.

As mentioned above lithified Pleistocene rocks crop out at various localities, especially in the northern part of the bay and provide hard substrate for benthic algae and a variety of invertebrates (Pl. 1, fig. 2).


Fig. 2: Oblique aerial photograph of inner part of Bahia la Choya. M: salt marsh; S: spit; IF: inner flat; MF: mid flat; C: channel.

DISTRIBUTION OF SEDIMENT

Sediment is patchily distributed within Bahia la Choya (Fig. 3). The bulk of the sediment accumulates in the southeastern, more protected part of the bay (thickness usually > 1 m, but probably less than 2–3 m). Over large areas of the northern, more exposed part of the bay sediment thickness is less than 15 cm. Frequently the underlying lithified Pleistocene crops out as rocky flats or small irregular patches or is covered by a thin veneer (2–3 cm) of sediment. Pleistocene outcrops are also widespread along the outermost reaches of the intertidal zone and extend into the shallow subtidal. In general, outcrops of Pleistocene influence sediment composition, grain size, sorting, carbonate content, and composition of molluscan communities. Net rates of sedimentation apparently are very low.

Fig. 3: Map of Bahia la Choya giving the burial depth of the Pleistocene rocky substrate. The southern part of the bay is predominantly sandy, whilst in the northern part Pleistocene rocks are exposed or covered only by a thin veneer of sediment. A–D: position of the four transects.
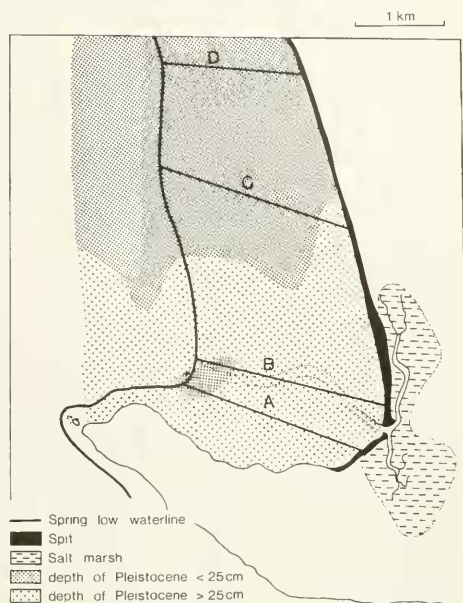
SEDIMENTS AND SEDIMENTARY STRUCTURES

Petrographic and sedimentological data collected along the four transects and from shallow subtidal stations are summarized in Figs 4–7. We describe here the petrographic composition, grain size, sorting, and physical and biogenic sedimentary structures of Bahia la Choya. From this information and from radiocarbon dates we infer rates of sedimentation.

PETROGRAPHIC COMPOSITION

The main constitutent of Bahia la Choya sediments is quartz, followed by skeletal carbonate grains, feldspar, rock fragments, heavy minerals, and mica. Sphericity of sand-sized quartz and feldspar grains varies from subangular to round. Rock fragments consist of reworked Pleistocene arkosic sandstones, granite or volcanic material. Granite fragments are frequently poorly rounded, and volcanics are invariably very well rounded. The sediment is arkosic indicating a close source area, most likely the immediate surroundings of Bahia la Choya.

GRAIN SIZE

The grain size ranges from silty fine sand to gravelly coarse sand. The dominant mode is fine sand. Transect A (Fig. 4) shows a decrease in grain size toward the shore which is typical of tidal flat sequences. The decrease in grain size is a result of diminishing water energy across the flat. A similar decrease exists along Transect B (Fig. 5), but is masked by input of coarser material close to shore from the adjacent spit. Transects C and D (Figs 6, 7) do not show such a zonation. This can be explained by their less protected setting and by abundant outcrops of lithified Pleistocene which greatly influence local grain size distribution patterns: Samples taken close to Pleistocene rocks have, on the whole, a larger grain size than samples taken at some distance. This indicates that present-day reworking of Pleistocene rocky flats substantially adds to the sediment in the immediate neighborhood of such outcrops. Pleistocene rocks in the vicinity of Bahia la Choya and on the flats themselves probably constitute an important source of sediment for the bay.

Due to its low percentage of mud, the tidal flat of Bahia la Choya is of the sandy type, the range in grain size being considerably smaller than, for instance, in the tidal flats of the northwestern coast of Germany (e. g. REINECK 1978).

CARBONATE CONTENT

The calcium carbonate content of the sediment varies between 1.5 % and 41 % (Figs 4–7). It consists of complete and broken shells as well as skeletal grains. Chief components are molluscs; minor constituents are echinoderms, red algae, bryozoans, forams, ostracods, serpulids, and barnacle plates.
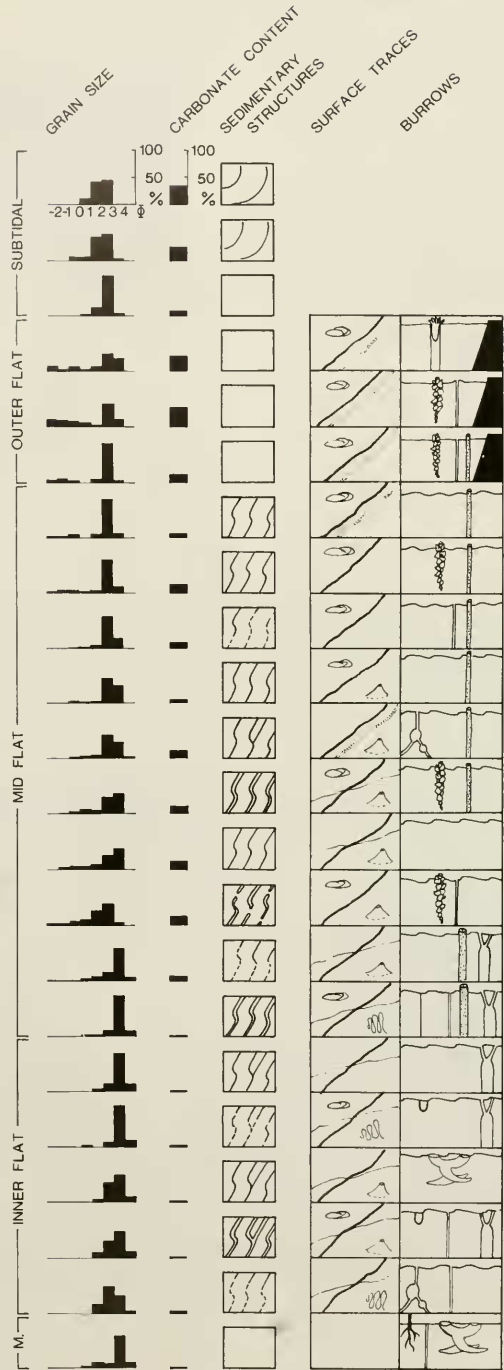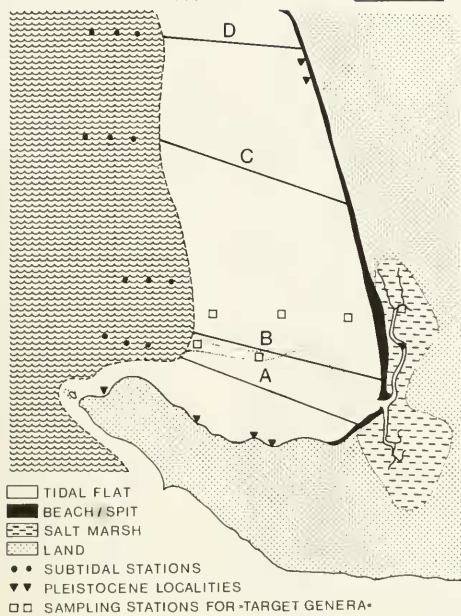
TRANSECT A

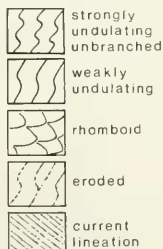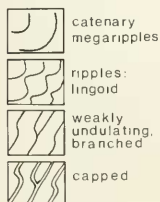Fig. 4:   Sedimentological and ichnological features of Transect A. For key see Fig. 5.
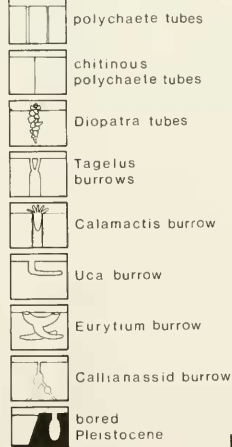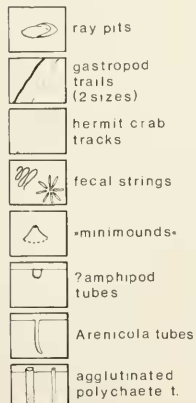
Fig. 5: a: Map of Bahia la Choya showing location of Transects A−D, subtidal stations, and Pleistocene localities. b: Sedimentological and ichnological features of Transect B.

Fig. 6: Sedimentological and ichnological features of Transect C. For key see Fig. 5.

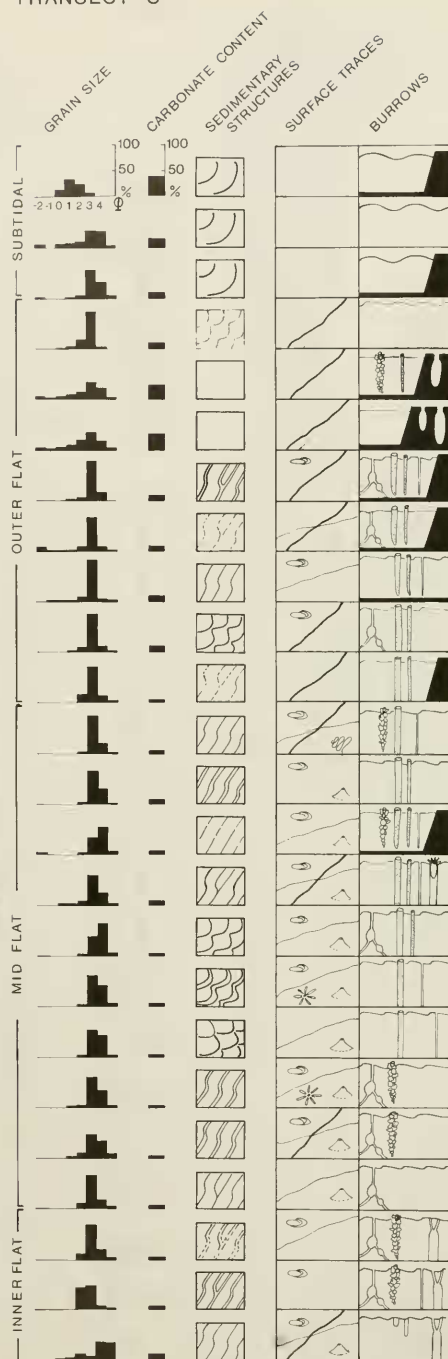The carbonate cement of Pleistocene rock fragments and re-worked Pleistocene shells contribute to the carbonate content of sediments near outcrops of Pleistocene.

In Transects A, C and to a lesser extend in D, there is a decrease in the percentage of carbonate landward. This trend is masked in Transect B where the input of skeletal debris and shells from the spit increases the carbonate content of the nearshore sediments. In addition, tidal channel sediments contain much more carbonate than surrounding flats (Fig. 5). The landward decrease in carbonate content is partly a function of grain size: silt-sized components rarely consist of carbonate. Calcium carbonate is concentrated in medium to coarse sand as well as in the gravel size range. As the grain size decreases landward, there is a corresponding decrease in the carbonate content. The overall higher carbonate content of shallow subtidal and outer flat sediments suggests these areas accumulate higher concentrations of skeletal carbonate.
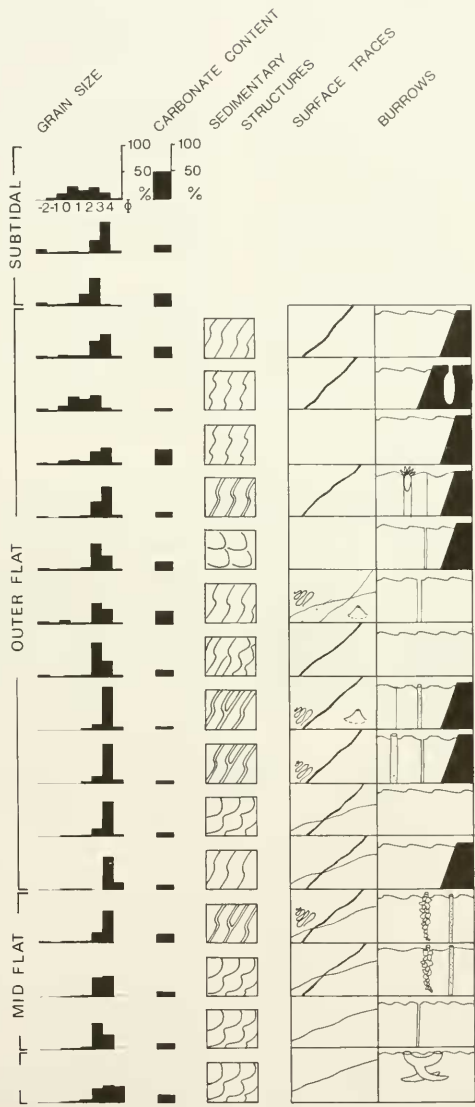
TRANSECT D

Fig. 7: Sedimentological and ichnological features of Transect D. For key see Fig. 5.

Carbonate content is also correlated with outcrops of Pleistocene rocks. This is partly due to the input of rock fragments with carbonate cement (see above), and partly to the low net rate of physical sedimentation, allowing a concentration of calcareous skeletal elements.

SORTING

The degree of sorting is generally good in the southern part of the bay and poorer in the northern part. Outer and mid flat areas are well sorted. Sorting is very poor in the tidal channel (Fig. 5) and close to outcrops of Pleistocene rocks. Thus, poor sorting is caused by either the concentration of shells in the channel sediments (Pl. 2, fig. 4), by eroded Pleistocene rock fragments, or by both.

PHYSICAL SEDIMENTARY STRUCTURES

Very shallow subtidal and outer flat areas are covered by a system of interdigitating sand waves (Fig. 1, Pl. 1, fig. 3). They have a wave length of 10 to 15 m and decrease in amplitude toward the mid flat where they finally disappear. Very coarse shell material accumulates in the troughs of the sand waves (Pl. 1, figs 1, 4). The shell material consists of reworked Pleistocene and Recent shells. Sediment size fines upward within the sand waves.

Undulatory megaripples occur in coarse to very coarse sediment of the estero channel and in shallow subtidal areas (e. g. pl. 3, fig. 1).

Small ripples (Pl. 3, fig. 3) are straight-crested or undulating, sometimes branch and are usually asymmetric. Except in some areas close to the beach they are ebb oriented. They are the most common physical sedimentary structure. They occur from the outer flat where they cover sand waves, to mid and inner flat areas. The fine-grained and partially algal bound sediment of the inner flat firmgrounds contain only poorly developed ripples (Pl. 3, fig. 2). The wave length of small ripples varies between 7 to 15 cm, and the direction of ripple crests varies between 0° and 45° (with a dominance of 20−25°). Many ripples have flattened tops, a typical feature caused by subaerial exposure. Most ripples are current ripples caused by tidal currents. Opposing currents sometimes change originally asymmetric ripples into symmetric ones. Others are probably the result of the combined influence of waves and currents. Interference ripples are rare.

Linguoid ripples are found in smaller tidal creeks as well as on the margin of the major tidal channel. They were also observed after storms on parts of the tidal flat (Pl. 3, fig. 4).

Current lineation occurs along the margins of the tidal channel of the mid flat.

The inventory of the physical sedimentary structure is typical of tidal flats (e. g. REINECK 1978; REINECK & SINGH 1980) and need not be discussed in detail.

BIOGENIC SEDIMENTARY STRUCTURES

Biogenic sedimentary structures are ubiquitous on the tidal flat of Bahia la Choya both in soft and hard substrate. They have been little studied in the past (e. g. EKDALE 1978, EKDALE et al. 1984, FLESSA & EKDALE 1987). As several ongoing studies at the University of Utah deal with ichnological aspects of the tidal flat and associated Pleistocene rocky substrates in detail, only a short summary of the most common types of traces and their sedimentological impact is given here.

ICHNOLOGICAL INVENTORY

The most conspicuous traces on the tidal flat are large feeding excavations of rays. The circular to semicircular pits are 5 to 15 cm deep and on average 30−50 cm in diameter. Commonly they are floored by shells and shell fragments (Pl. 4, fig. 3). Feeding traces of rays contribute considerably to sediment reworking (e. g. GRANT 1983). The activities of rays are thought to be, together with the burrowing activity of callianassid shrimps (see below), largely responsible for the destruction of physical sedimentary structures on the tidal flat. In addition, rays are important agents of shell bed formation as finer sediment particles are winnowed and carried away by tidal·currents during excavation, leaving a shell lag behind.

The feeding activity of rays may also be one factor in producing the mesita-like relief of the inner flat firmground. The rays may disrupt the stabilized, algal bound surface layer. Pits created this way are subsequently enlarged by erosion by waves and currents.

Crawling traces of gastropods are widespread and occur in various size classes. Most abundant are trails 1−2 mm in diameter made by various species of Nassarius and trails 5 mm in diameter created by Cerithidea and less commonly by Cerithium (Pl. 5, fig. 1). The trails are shallow grooves bordered on both sides by sediment ridges. Their preservation potential is low except on the inner flat firmground.

Trackways of arthropods, consisting of imprints of the podia, are common on mid flat areas where most are made by hermit crabs (Pl. 4, fig. 5).

Resting traces of the sea anemone Calamactis occur scattered across outer and mid flat areas and are characterized by a vertical tube surrounded by radial grooves (Pl. 4, fig. 2).

Fecal strings of various sizes are found occasionally on outer and mid flat areas. Some of them may have been made by the polychaete Arenicola, although none of the characteristic U- or J-shaped burrows were found associated with them.

Callianassid burrows (Pl. 4, figs 1, 6) are very abundant. They are made by *Callianassa* and *Upogebia* (FLESSA & EKDALE 1987) and typically exhibit smooth, lined burrow walls. Burrows of the former have the characteristic swollen branching points of many callianassid burrows, whilst those of the latter are more frequently branched and form an intricate boxwork (FLESSA & EKDALE 1987). Associated with the burrows are small cones of sediment on the surface which consist of material expelled by the shrimps from their burrows.

Crab burrows (Pl. 5, figs 2, 5; Pl. 8, fig. 2) usually have a greater burrow diameter than shrimp burrows. Two main types are common: Unbranched, J-shaped burrows, 2−3 cm in diameter, made by the fiddler crab *Uca*. The burrow openings are frequently surrounded by sand pellets which represent either material expelled from the burrows or pellets created during their feeding process on the sediment surface (Pl. 5, fig. 5). The second burrow type, excavated by the crab *Eurytium*, is 3−5 cm in diameter and branched.

Small, vertical, U-shaped burrows with a tube diameter of 1−2 mm and an observed depth of 5 cm are inhabited by small, amphipod-like crustaceans (Pl. 5, fig. 4).

Very widespread are straight vertical tubes, most of them are probably inhabited by polychaetes. Some are unlined, others have a thin (1 mm thick) agglutinated burrow wall and are constructed by the polychaete *Onuphis* (EKDALE et al. 1984, fig. 7−2). In yet others the agglutinated burrow wall is 2−3 mm thick. In both types the wall material consists of sand-sized particles. Tubes of the polychaete *Diopatra*, in contrast, have very coarsely agglutinated burrow walls, and most particles consist of shell fragments. Very thin (1 mm ∅) chitinous tubes constitute a fourth type of straight vertical tubes.

The preservation potential of bivalve burrows is usually low. An exception are the burrows of *Tagelus*, a deep infaunal bivalve whose burrow may reach up to five times the length of the animal (5−10 cm). The burrow is oval in cross-section and bifurcates toward the sediment surface indicating

ZONATION OF BIOGENIC SEDIMENTARY STRUCTURES

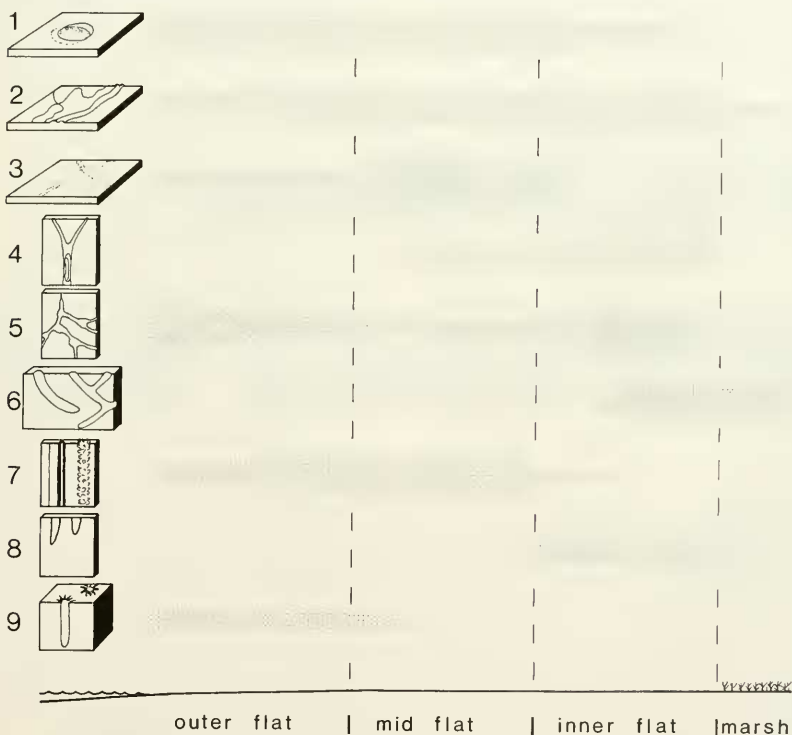outer flat | mid flat | inner flat | marsh

Fig. 8: Zonation of biogenic sedimentary structures across the tidal flat. 1: ray pits; 2: gastropod trails; 3: hermit crab tracks; 4: *Tagelus* burrows; 5: callianassid burrows; 6: crab burrows; 7: unlined, heavily lined and agglutinated vertical tubes of polychaetes; 8: ?amphipod U-tubes; 9: resting traces of sea anemones. Thickness of bars indicates relative abundance.

the presence of long siphons (Pl. 4, fig. 4). It can be recognized on the sediment surface by the presence of paired openings.

Exposed Pleistocene rocks exhibit a number of boring organisms. Most common are the flask-shaped borings of the bivalve *Lithophaga* and the club- to J-shaped borings of the sipunculid worms *Phascolosoma* and *Themiste* (FLESSA & EKDALE 1987). The numerous boring organisms occurring in shell material across the tidal flat are described in detail by FEIGE & FÜRSICH (this volume).

DISTRIBUTION ACROSS THE TIDAL FLAT
(Figs 4–8)

A number of traces occur throughout the tidal flat, among them ray pits, gastropod trails, callianassid burrows and vertical tubes. In the latter two, however, the density varies between subenvironments. Agglutinated tubes are most common in outer to mid flat areas, whilst callianassid burrows have their highest density close to the shore. Some other traces are confined to particular parts of the tidal flat: *Tagelus* and ?amphipod burrows are found in the inner flat and inner mid flat only. *Uca* and *Eurytium* burrows are confined to the inner flat, salt marsh and estero channel. Hermit crab tracks occur only in outer and mid flat areas.

On the whole, the zonation of biogenic sedimentary structures is not very pronounced (Fig. 8). Still, it allows differentiation of two major areas, the outer/mid flat and the inner flat/salt marsh.

RATES OF SEDIMENTATION

The very low thickness of Holocene sediments overlying lithified late Pleistocene sediments suggests very low net rates of sedimentation within Bahia la Choya. These rates are slightly higher in the southern part of the bay as opposed to the northern part where Pleistocene rocky flats are exposed over large areas. Radiocarbon dates of shells (MELDAHL 1987)

confirm this view: For example, a large *Dosinia* shell, collected from the surface of the outer flats in the northern part of the bay gave an age of 3230 +/−75 years. A *Chione* shell collected at a depth of 60 cm in the outer flat area of Transect B revealed an age of 4250 +/−80 years. Shells from mid and inner flat areas collected at a depth of 48 and 126 cm yielded an
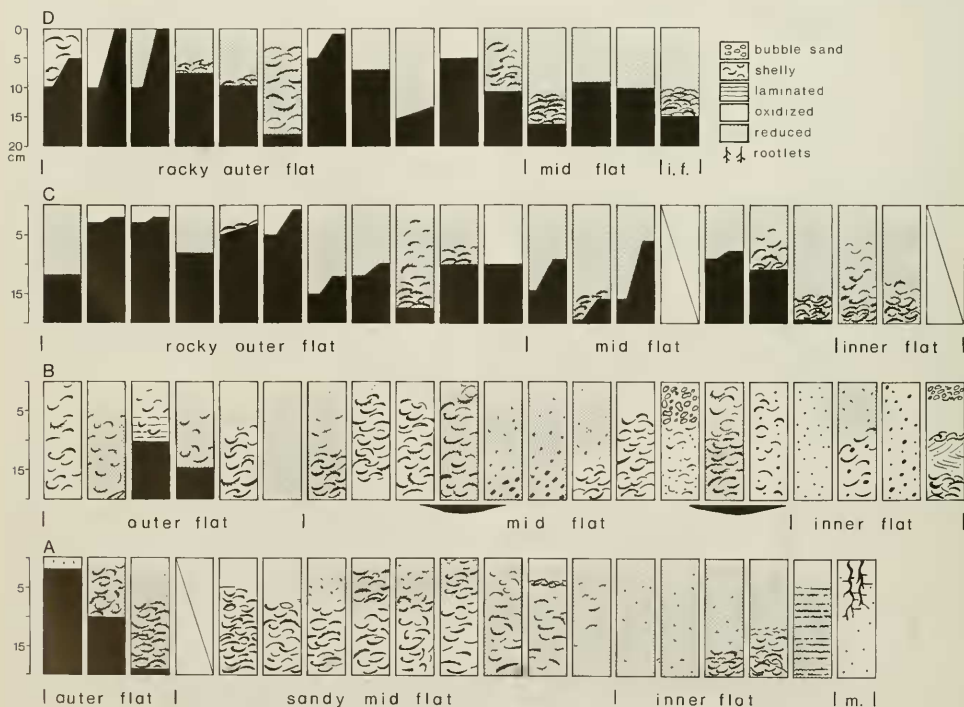

Fig. 9: Biofabric and depth of PRD layer (O_2/H_2S interface) in box cores taken along the four transects.

age of 2260 +/−75 and 2600 +/−145 years respectively. These dates suggest that in-situ reworking is a very common process at Bahia la Choya. The fact that shells recovered from the sediment surface are as old as those from within the sedi- ment indicates extensive vertical mixing of shells. The mollus- can taphocoenoses can therefore be regarded as highly time- averaged assemblages.

VERTICAL ZONATION OF SEDIMENTS

In order to learn more about biofabric, depth of oxidation zone, and internal sedimentation structures, box cores were taken from characteristic subenvironments. Selected samples are shown in Pl. 6. In addition, at each sampling point along the four transects internal features of the sediment to a depth of about 20 cm were noted. The results are shown in Fig. 9.

In general, very few physical sedimentary structures are preserved. Exceptions are crossbedding (seen as internal fea- ture of megaripples within the estero channel) and bubble sand (Pl. 5, fig. 3) near the beach. The latter is a result of en- trapment of air caused by rapid flooding of sand (e. g. REINECK 1956) and is a good indicator of deposition on foreshore or si- milar environments (REINECK & SINGH 1980). Remains of la- mination are often preserved in the uppermost few centime- tres of inner flat firmgrounds (Pl. 6, fig. 2).

In Transects C and D sediment cover is very thin (Fig. 9). In Transects A and B shell beds are very abundant within the uppermost 20 cm of sediment. They occupy most of the ob- served cross-section in outer and mid flat areas. Shell beds vary in thickness from 2 to >20 cm and have gradational or sharp boundaries. There is no preferred orientation of skeletal elements within shell beds.

The depth of the reduced zone varies between 0,2 and >20 cm and is most commonly between 2 and 5 cm. In se- veral cases, a reduced layer is sandwiched between two ox- idized layers. In these instances the lower oxidized layer is invariably shelly. Quite clearly, the position of the reduction zone is greatly influenced by the permeability of the sedi- ment. The position of the reduced layer within 1 to 3 cm of the sediment-water interface in inner mid flat to inner flat sediments of Transect A points to a very stable sediment and very little sediment input.

Bioturbation by a variety of organisms (see above) and, in the case of the salt marsh, by plants is responsible for the scar- city of primary sedimentary structures (e. g. Pl. 5, fig. 2, Pl. 6). The thorough bioturbation of the sediment is further evidence of low rates of sedimentation and physical rework- ing. Reworking processes play a major role in the sedimenta- tion history of Bahia la Choya and apparently are largely bio- logically controlled.

SUMMARY OF MAJOR HABITATS OF BAHIA LA CHOYA

According to sediment type, physical and biogenic sedi- mentary structures, vegetation, and topography, the tidal flat complex of Bahia la Choya can be subdivided into several subenvironments or habitats.

Little is known about the very shallow subtidal zone at Bahia la Choya. Scuba diving and limited grab sampling to a water depth of 7 m indicated both sandy substrate with me- garipples and rocky Pleistocene with sand patches inbetween − seaward extensions of the low intertidal habitats.

Outer tidal flats (Pl. 1) are characterized by sand waves the tops of which are covered by current ripples, whilst in the troughs coarse shell material accumulates. Grain size varies from fine to medium sand. Carbonate content is relatively high. Bioturbation structures are dominated by polychaete tubes and burrows of callianassid shrimps. The surface is co- vered by ray pits and gastropod trails. Where the sediment co- ver is very thin, extensive rocky flats exist with soft sediment occurring in pockets or forming a thin algally stabilized ve- neer on top. The rocky flats are extensively bored and en- crusted and support (in contrast to the sandy flats) a varied epifauna.

The outer flat grades, without noticeable break, into the sandy mid flat (Pl. 3, fig. 3). Current or combined wave/ current ripples cover the largely flat area of fine sand. Biotur- bation is very similar to that of the outer flat, the carbonate content is usually lower.

There is a distinct break from the mid to the inner flat. The latter is characterized by silty fine sand and a rather firm substrate with poorly developed ripples (Pl. 3, fig. 2). The carbonate content is low. Due to patchy erosion, the sediment surface exhibits a mesita-like topography (Pl. 7, fig. 4). Bio- turbation is extensive and is caused by callianassid shrimps and by crabs.

The salt marsh (Pl. 7, fig. 2) is vegetated with halophytes (Salicornia, Sueda, and Distichlis) and thoroughly burrowed by crabs (Uca, Eurytium). The fine-grained sediment is poorly sorted.

The tidal channel (Pl. 7, figs 1, 3) is broad and shallow across the flat, but narrows and becomes deeper where it cuts through the shelly spit separating marsh (estero) from tidal flat. In the marsh the channel splits into two major branches which in turn anastomose. Megaripples (Pl. 3, fig. 1) and coarse sandy sediment characterize the channel in the estero, whilst poorly sorted gravelly to sandy sediment, shell pave- ments, and gravel bars are typical of mid to outer channel areas. Shells are preferentially oriented downstream (Pl. 8, fig. 4) and current lineation is commonly observed along the banks (Pl. 8, fig. 3).

A shelly spit, up to 3 m high and with a maximum width of 100 m, separates the tidal flat from the marsh (Fig. 2, Pl. 8, fig. 5). it consists nearly exclusively of shells and shell debris which have a mixed origin – some are subtidally derived, others come from the marsh. Where the channel cuts through the spit, its shell material is reworked and transported along the channel onto the tidal flat. Most of it is deposited as a sediment apron where the channel enters the tidal flat. The remaining material is transported further seaward and becomes incorporated into the taphocoenoses of Bahia la Choya.

THE MOLLUSCAN FAUNA

PREVIOUS WORK

Because of its close vicinity to the United States, the Puerto Peñasco area has been visited by numerous malacologists and amateur collectors. LOWE (1934) gave a first general account of a trip to Puerto Peñasco and a year later recorded 299 species found at that locality (LOWE 1935). In the following years Puerto Peñasco and Bahia la Choya were visited repeatedly which resulted in descriptions of new species (e. g. BERRY 1945, 1956a, b, 1957, 1958, 1960, 1964; DUSHANE & MCLEAN 1968, MARCUS & MARCUS 1967). KEEN (1947) added 61 species to LOWE's (1935) list; RICE (1966) lists 52 species from Bahia la Choya. Lists of individual groups were given by BURCH (1967a, b) for the Muricidae and Olividae, and by JOHNSON (1968) for the Conidae. Descriptions of Bahia la Choya are scarce and cursory (BERRY 1955, DUSHANE 1957). BERRY's (1955) account is a short, but colorful description of the main habitats of Bahia la Choya and the corresponding molluscan faunas.

These earlier surveys were not very systematic and the present study is the first comprehensive account of the molluscan fauna of Bahia la Choya and its distribution in various habitats.

Table 1. List of mollusc shells found in the shallow subtidal, on the tidal flat, and in the salt marsh at Bahia la Choya.

BIVALVIA

Nuculidae
Nucula declivis HINDS 1843

Nuculanidae
Nuculana (Saccella) elenensis (SOWERBY 1833)

Arcidae
Arca (Arca) mutabilis (SOWERBY 1833)
A. (A.) pacifica (SOWERBY 1833)
Barbatia (Acar) rostae BERRY 1954
B. (Calloarca) alternata (SOWERBY 1833)
B. (Fugleria) illota (SOWERBY 1833)
Anadara (Larkinia) multicostata (SOWERBY 1833)
Arcopsis solida (SOWERBY 1833)

Glycymeridae
Glycymeris (Glycymeris) gigantea (REEVE 1843)
G. (Tucetona) multicostata (SOWERBY 1833)

Mytilidae
Brachidontes semilaevis (MENKE 1849)
Mytella guyanensis (LAMARCK 1819)
Gregariella coarctata (CARPENTER 1857)
Lithophaga (Labis) attenuata (DESHAYES 1836)
L. (Leiosolenus) abbotti LOWE 1935
Modiolus capax (CONRAD 1837)

Pteriidae
Pteria sterna (GOULD 1851)

Isognomidae
Isognomon janus CARPENTER 1857

Ostreidae
Saccostrea palmula (CARPENTER 1857)
Lopha angelica (ROCHEBRUNE 1895)
Crassostrea corteziensis (HERTLEIN 1951)

Pectinidae
Pecten (Oppenheimopecten) vogdesi ARNOLD 1906
Argopecten circularis (SOWERBY 1935)
Cyclopecten pernomus (HERTLEIN 1935)
Leptopecten (Leptopecten) velero (HERTLEIN 1935)

Limidae
Lima (Promantellum) pacifica D'ORBIGNY 1846

Anomiidae
Anomia adamas GRAY 1850

Crassatellidae
Crassinella pacifica (C. B. ADAMS 1852)
C. adamsi OLSSON 1961

Cardiidae
Cardita (Byssomera) affinis SOWERBY 1833
C. (Cardites) sp.

Lucinidae
Lucina (Callucina) lampra (DALL 1901)
L. (Lucinisca) centrifuga (DALL 1901)
Parvilucina (Parvilucina) approximata (DALL 1901)
P. (P.) mazatlanica (CARPENTER 1855)
P. (Cavilinga) prolongata (CARPENTER 1857)
Ctena mexicana (DALL 1901)
Divalinga (Divalinga) ebumea (REEVE 1850)

Ungulinidae
Diplodonta orbella (GOULD 1852)
D. subquadrata (CARPENTER 1856)
Felaniella (Zemysia) sericata (REEVE 1850)
Phlyctiderma (Phlyctiderma) discrepans (CARPENTER 1857)

Galeommatidae
Galeommella peruviana (OLSSON 1961)
Galeommella sp. A
Tryphomyax mexicanus (BERRY 1959)

Leptonidae
Solecardia eburnea CONRAD 1849

Montacutidae
Aligena cokeri DALL 1909
Orobitella obliqua (HARRY 1969)
O. trigonalis (CARPENTER 1857)
O. cf. *zorrita* OLSSON 1961

Sportellidae
Basterotia (Basterotella) hertleini DURHAM 1950

Chamidae
Chama mexicana CARPENTER 1857
C. frondosa BRODERIP 1835
Pseudochama saavedrai HERTLEIN & STRONG 1946

Cardiidae
Trachycardium (Trachycardium) concors (SOWERBY 1833)
T. (Mexicardia) panamense (SOWERBY 1833)
Papyridea aspersa (SOWERBY 1833)
Trigoniocardia (Trigoniocardia) granifera
    (BRODERIP & SOWERBY 1829)
T. (Americardia) biangulata (BRODERIP & SOWERBY 1829)
Laevicardium elatum (SOWERBY 1833)
L. elenense (SOWERBY 1840)

Veneridae
Tivela (Tivela) byronensis (GRAY 1838)
Pitar (Pitar) helenae OLSSON 1961
P. (Lamelliconcha) concinnus (SOWERBY 1835)
Megapitaria squalida (SOWERBY 1835)
Dosinia dunkeri (PHILIPPI 1844)
D. ponderosa (GRAY 1838)
Chione (Chione) californiensis (BRODERIP 1835)
C. (Chionista) fluctifraga (SOWERBY 1853)
C. (Chionopsis) gnidia (BRODERIP & SOWERBY 1828)
C. (C.) purpurissata DALL 1902
C. (C.) pulicaria (BRODERIP 1835)
C. (Lirophora) mariae (D'ORBIGNY 1846)
C. (Timoclea) squamosa (CARPENTER 1857)
Protothaca (Tropithaca) grata (SAY 1831)

Petricolidae
Petricola (Petricola) exarata (CARPENTER 1857)
P. (P.) lucasana HERTLEIN & STRONG 1948
P. (Rupellaria) denticulata SOWERBY 1834

Cooperellidae
Cooperella subdiaphana (CARPENTER 1864)

Mactridae
Mactra (Mactrotoma) nasuta GOULD 1851
M. (Micromactra) californica CONRAD 1837
Raeta undulata (GOULD 1851)

Tellinidae
Tellina (Angulus) meropsis DALL 1900
T. (A.) amianta DALL 1900
T. (A.) carpenteri DALL 1900
T. (A.) coani KEEN 1971
T. (Eurytellina) simulans C. B. ADAMS 1852
T. (Laciolina) ochracea CARPENTER 1864
T. (Merisca) brevirostris DESHAYES 1855
T. (M.) rhynchoscuta (OLSSON 1961)
T. (Tellinella) cumingii argis OLSSON 1971
Leporimetis (Florimetis) cognata (PILSBRY & VANATTA 1902)
Macoma (Rexithaerus) indentata CARPENTER 1864
Strigilla (Pisostrigilla) interrupta MOERCH 1860
Tellidora burneti (BRODERIP & SOWERBY 1829)

Donacidae
Donax gracilis HANLEY 1845
D. navicula HANLEY 1845

Psammobiidae
Heterodonax pacificus (CONRAD 1837)

Solecurtidae
Tagelus (Tagelus) affinis (C. B. ADAMS 1852)
T. (T.) californianus (CONRAD 1837)
T. (Mesopleura) politus (CARPENTER 1857)

Semelidae
Semele flavescens (GOULD 1851)
S. guaymasensis PILSBRY & LOWE 1932
S. jovis (REEVE 1853)
S. pacifica DALL 1915
Cumingia adamsi OLSSON 1961 ex CARPENTER MS
C. lamellosa SOWERBY 1833
C. pacifica DALL 1915

Solenidae
Solen (Solen) rosaceus CARPENTER 1864

Myidae
Cryptomya californica (CONRAD 1837)
Sphenia fragilis (H. & A. ADAMS 1854)

Corbulidae
Corbula (Caryocorbula) marmorata HINDS 1843
C. (Juliacorbula) bicarinata SOWERBY 1833
C. (J.) biradiata SOWERBY 1833

Gastrochaenidae
Gastrochaena ovata SOWERBY 1834

Hiatellidae
Hiatella arctica (LINNE 1767)

Pandoridae
Pandora (Pandora) uncifera PILSBRY & LOWE 1932

Lyonsiidae
Entodesma (Phlycticoncha) lucasanum
       (BARTSCH & REHDER 1939)

Thraciidae
Thracia curta CONRAD 1837
T. squamosa CARPENTER 1857
Cyathodonta lucasana DALL 1915
C. dubiosa DALL 1915
Asthenothaerus villosior CARPENTER 1864

GASTROPODA

Fissurellidae
Diodora inaequalis (SOWERBY 1835)
D. alta (C. B. ADAMS 1852)
Lucapinella milleri BERRY 1959

Acmaeidae
Collisella acutapex (BERRY 1960)
C. turveri (HERTLEIN & STRONG 1951)

Trochidae
Calliostoma marshalli LOWE 1935
Tegula (Agathistoma) mariana DALL 1919
T. (Chlorostoma) rugosa (A. ADAMS 1853)

Liotiidae
Arene (Otollonia) fricki (CROSSE 1865)

Turbinidae
Turbo (Callopoma) fluctuosus WOOD 1828

Neritidae
Nerita (Theliostyla) funiculata MENKE 1851
Theodoxus (Vittoclithon) luteofasciatus MILLER 1879

Phenacolepadidae
Phenacolepas osculans (C. B. ADAMS 1852)

Littorinidae
Littorina aspera PHILIPPI 1846

Vitrinellidae
Teinostoma sp.

Turritellidae
Turritella anactor BERRY 1957
T. gonostoma VALENCIENNES 1832
T. leucostoma VALENCIENNES 1832
Vermicularia frisbeyae MCLEAN 1970
V. pellucida eburnea (REEVE 1842)

Modulidae
Modulus disculus (PHILIPPI 1846)

Vermetidae
Vermetus (Thylaeodus) indentatus (CARPENTER 1857)
Tripsycha (Tripsycha) tripsycha (PILSBRY & LOWE 1932)
T. (Eualetes) centiquadra (VALENCIENNES 1846)
Dendropoma lituella (MOERCH 1861)

Cerithiidae
Cerithium (Thericium) stercusmuscarum VALENCIENNES 1833

Potamididae
Cerithidea mazatlanica CARPENTER 1857

Epitoniidae
Epitonium (Nitidiscala) hindsii (CARPENTER 1856)
E. (N.) barbarinum DALL 1919
Alora gouldii (A. ADAMS 1857)

Hipponicidae
Hipponix panamensis C. B. ADAMS 1852
H. pilosus (DESHAYES 1832)

Calyptraeidae
Calyptraea (Calyptraea) mamillaris BRODERIP 1834
Crepidula excavata (BRODERIP 1834)
C. incurva (BRODERIP 1834)
C. lessonii (BRODERIP 1834)
C. onyx SOWERBY 1824
C. rostrata C. B. ADAMS 1852
C. striolata MENKE 1851
C. uncata MENKE 1847
Crucibulum (Crucibulum) ignarium (BRODERIP 1834)
C. (C.) scutellatum (WOOD 1828)
C. (C.) spinosum (SOWERBY 1824)
C. (Dispotaea) concameratum REEVE 1859
C. (D.) serratum (BRODERIP 1834)

Naticidae
Natica (Natica) chemnitzii PFEIFFER 1840
Polinices (Polinices) uber (VALENCIENNES 1832)
Neverita (Glossaulax) reclusiana (DESHAYES 1939)

Cymatiidae
Cymatium (Turritriton) gibbosum (BRODERIP 1833)

Buccinidae
Solenosteira macrospira BERRY 1957
Phos (Cymatophos) fusoides (C. B. ADAMS 1852)
P. (C.) dejanira (DALL 1919)

Columbellidae
Columbella strombiformis LAMARCK 1822
Anachis (Costoanachis) adelinae (TRYON 1883)
A. (C.) nigricans (SOWERBY 1844)
A. (?C.) sanfelipensis LOWE 1935
A. (C.) varia (SOWERBY 1832)

Mitrella xenia (DALL 1919)
Parametaria dupontii (KIENER 1849-50)
Strombina (Strombina) sp.

Melongenidae
Melongena patula (BRODERIP & SOWERBY 1828)

Nassariidae
Nassarius (Nassarius) guaymasensis (PILSBRY & LOWE 1932)
N. (N.) versicolor (C. B. ADAMS 1852)
N. (Phrontis) iodes (DALL 1917)
N. (P.) brunneostoma (STEARNS 1893)
N. (P.) tiarula (KIENER 1841)

Fasciolariidae
Fusinus sp.

Olividae
Oliva (Oliva) incrassata [LIGHTFOOT 1786]
O. (O.) spicata (ROEDING 1798)
Agaronia testacea (LAMARCK 1811)
Olivella (Olivella) dama (WOOD 1928 ex MAWE, MS)

Conidae
Conus (Leptoconus) regularis SOWERBY 1833
C. (L.) scalaris VALENCIENNES 1832
C. (Ximeniconus) perplexus SOWERBY 1857

Terebridae
Terebra armillata HINDS 1844
T. elata HINDS 1844

Turridae
Agladrillia pudica (HINDS 1843)
Crassispira (Striospira) kluthi E. K. JORDAN 1936
Pilsbryspira (Pilsbryspira) garciacubasi SHASKY 1971
P. (Nymphispira) bacchia (DALL 1919)

Pyramidellidae
Pyramidella (Longchaeunus) mazatlanica
          DALL & BARTSCH 1909

Bullidae
Bulla (Bulla) gouldiana PILSBRY 1895

Scaphandridae
Acteocina inculta (GOULD & CARPENTER 1857)

Melampidae
Melampus (Melampus) mousleyi BERRY 1964
Pedipes unisculcatus COOPER 1866

SCAPHOPODA

Dentaliidae
Tesseracme quadrangulare (SOWERBY 1832)
Graptacme semipolitum (BRODERIP & SOWERBY 1829)

Laevidentaliidae
Laevidentalium splendidum (SOWERBY 1832)

GENERAL FEATURES

Hard-shelled taxa are dominated by molluscs. Other groups present include barnacles, rare brachiopods (Glottidia), bryozoans, serpulids, echinoderms, foraminifera, and ostracods. They have been identified using BRUSCA (1980). Of these invertebrate groups, bryozoans are diverse, and the echinoids are conspicuous, being represented by 3 species: Encope grandis, E. micropora, and Mellita longifissa. In most samples these groups constitute less than 3 % in terms of relative abundance and have therefore been neglected except for the taphonomic analysis.

From the very shallow subtidal (which has been sampled only very cursorily) to the supratidal, 218 species of molluscs have been recorded, among them 127 species of bivalves, 88 of gastropods and 3 of scaphopods. The mollusc fauna was identified using BECKVAR et al. (1985), KEEN (1971), KEEN & COAN (1976) and OLSSON (1961). A comprehensive faunal list is given in Table 1. Table 2 lists information on feeding modes and life habits of the individual species (see also Fig. 10).

Common elements of the molluscan fauna are figured on Pls. 9 and 10. Data on the autecology are based, where possible, on our own observations or on information from the literature (especially information in KEEN [1971] and MORRIS et al. [1980]). Among the bivalves, most species are infaunal suspension-feeders, whilst among the gastropods epifaunal detritus-feeders and herbivores prevail.

The diverse mollusc fauna belongs to the tropical Panamic faunal province which ranges from the northern Gulf of California southward to Panama (KEEN 1971). The relatively high diversity, compared to temperate settings such as the North Sea, of these high stress environments make Bahia la Choya an ideal area to study onshore-offshore variations in diversity, faunal composition, life habit groups, and taphonomic features. As the final goal of the study is to learn more about the paleoecological significance of molluscan taphocoenoses, particular emphasis is laid on the distribution pattern of dead shells and their relation to environmental parameters.

Table 2. Substrate preference, mode of life, and mode of feeding of the shelly molluscan fauna of Bahia la Choya. H: preference for hard substrate; S: preference for soft substrate; L: mode of life; i: infaunal; is: shallow infaunal; id: deep infaunal; im: infaunal mobile; ib: endobyssate; bo: boring; e: epifaunal; em: epifaunal mobile; eb: epibyssate; ec: epifaunal cemented;   T: mode of feeding (trophic group); d: detritus/deposit-feeder; s: suspension-feeder; o: omnivore; c: carnivore; h: herbivore.

BIVALVIA	H	S	L	T
Nucula declivis		*	im	d
Nuculana (Saccella) elenensis		*	im	d
Arca (Arca) mutabilis	*		eb	s
A. (A.) pacifica	*		eb	s
Barbatia (Acar) rostae	*		eb	s
B. (Calloarca) alternata	*		eb	s
B. (Fugleria) illota	*		eb	s
Anadara (Larkinia) multicostata	*		eb	s
Arcopsis solida	*		eb	s
Glycymeris (Glycymeris) gigantea		*	is	s
G. (Tucetona) multicostata		*	is	s
Brachidontes semilaevis	*		eb	s
Mytella guyanensis		*	eb	s
Gregariella coarctata	*		ib	s
Lithophaga (Labis) attenuata	*		bo	s
L. (Leiosolenus) abbotti	*		bo	s
Modiolus capax	*		eb	s
Pteria sterna	*		eb	s
Isognomon janus	*		eb	s
Saccostrea palmula	*		ec	s
Lopha angelica	*		ec	s
Crassostrea corteziensis	*		ec	s
Pecten (Oppenheimopecten) vogdesi		*	em	s
Argopecten circularis		*	em	s
Cyclopecten pernomus		*	eb	s
Leptopecten (Leptopecten) velero		*	em	s
Lima (Promantellum) pacifica		*	eb	s
Anomia adamas	*		ec	s
Crassinella pacifica		*	is	s
C. adamsi		*	is	s
Cardita (Byssomera) affinis	*		eb	s
C. (Cardites) sp.	*		eb	s
Lucina (Callucina) lampra		*	id	s
L. (Lucinisca) centrifuga		*	id	s
Parvilucina (P.) approximata		*	id	s
P. (P.) mazatlanica		*	id	s
P. (Cavilinga) prolongata		*	id	s
Ctena mexicana		*	id	s
Divalinga (Divalinga) eburnea		*	id	s
Diplodonta orbella		*	is	s
D. subquadrata		*	is	s
Felaniella (Zemysia) sericata		*	id	s
Phlyctiderma (P.) discrepans	*		is	s
Galeommella peruviana		*	?	s
Galeommella sp. A		*	?	s
Tryphomyax mexicanus		*	?	s
Solecardia eburnea		*	?	s
Aligena cokeri		*	?	s
Orobitella obliqua		*	?	s
O. trigonalis		*	?	s

O. cf. zorrita		*	?	s
Basterotia (B.) hertleini	*		eb	s
Chama mexicana	*		ec	s
C. frondosa	*		ec	s
Pseudochama saavedrai	*		ec	s
Trachycardium (T.) concors		*	is	s
T. (Mexicardia) panamense		*	is	s
Papyridea aspersa		*	is	s
Trigoniocardia (T.) granifera		*	is	s
T. (Americardia) biangulata		*	is	s
Laevicardium elatum		*	is	s
L. elenense		*	is	s
Tivela (Tivela) byronensis		*	is	s
Pitar (Pitar) helenae		*	is	s
P. (Lamelliconcha) concinnus		*	is	s
Megapitaria squalida		*	is	s
Dosinia dunkeri		*	is	s
D. ponderosa		*	is	s
Chione (Chione) californiensis		*	is	s
C. (Chionista) fluctifraga		*	is	s
C. (Chionopsis) gnidia		*	is	s
C. (C.) purpurissata		*	is	s
C. (C.) pulicaria		*	is	s
C. (Lirophora) mariae		*	is	s
C. (Timoclea) squamosa		*	is	s
Protothaca (Tropithaca) grata		*	is	s
Petricola (Petricola) exarata	*		ib	s
P. (P.) lucasana	*		ib	s
P. (Rupellaria) denticulata	*		ib	s
Cooperella subdiaphana		*	is	s
Mactra (Mactrotoma) nasuta		*	is	s
M. (Micromactra) californica		*	is	s
Raeta undulata		*	is	s
Tellina (Angulus) meropsis		*	id	d
T. (A.) amianta		*	id	d
T. (A.) carpenteri		*	id	d
T. (A.) coani		*	id	d
T. (Eurytellina) simulans		*	id	d
T. (Laciolina) ochracea		*	id	d
T. (Merisca) brevirostris		*	id	d
T. (M.) rhynchoscuta		*	id	d
T. (Tellinella) cumingii argis		*	id	d
Leporimetis (Florimetis) cognata		*	id	d
Macoma (Rexithaerus) indentata		*	id	d
Strigilla (Pisostrig.) interrupta		*	id	d
Tellidora burneti		*	id	d
Donax gracilis		*	is	s
D. navicula		*	is	s
Heterodonax pacificus		*	is	s
Tagelus (Tagelus) affinis		*	id	s
T. (T.) californianus		*	id	s
T. (Mesopleura) politus		*	id	s
Semele flavescens		*	id	d
S. guaymasensis		*	id	d
S. jovis		*	id	d
S. pacifica		*	id	d
Cumingia adamsi		*	if	d
C. lamellosa		*	if	d

C. pacifica	*	if	d
Solen (Solen) rosaceus	*	is	s
Cryptomya califomica	*	is	s
Sphenia fragilis	*	ib	s
Corbula (Caryocorbula) marmorata	*	ib	s
C. (Juliacorbula) bicarinata	*	ib	s
C. (J.) biradiata	*	ib	s
Gastrochaena ovata	*	bo	s
Hiatella arctica	*	ib	s
Pandora (Pandora) uncifera	*	?	?
Entodesma (Phlycticoncha)			
lucasanum	*	eb	s
Thracia curta	*	is	s
T. squamosa	*	is	s
Cyathodonta lucasana	*	?	?
C. dubiosa	*	?	?
Asthenothaerus villosior	*	?	?

GASTROPODA

Diodora inaequalis	*	em	o/h
D. alta	*	em	0/h
Lucapinella milleri	*	em	h
Collisella acutapex	*	em	h
C. turveri	*	em	h
Calliostoma marshalli	*	em	o?
Tegula (Agathistoma) mariana	*	em	h
T. (Chlorostoma) rugosa	*	em	h
Arene (Otollonia) fricki	*	em	h
Turbo (Callopoma) fluctuosus	*	em	h
Nerita (Theliostyla) funiculata	*	em	h
Theodoxus (Vittoclithon)			
luteofasciatus	*	em	h
Phenacolepas osculans	*	em	h?
Littorina aspera	*	em	h
Teinostoma sp.?	?	em	h
Turritella anactor	*	is	s
T. gonostoma	*	is	s
T. leucostoma	*	is	s
Vermicularia frisbeyae	*	e	s
V. pellucida ebumea	*	e	s
Modulus disculus	*	em	?
Vermetus (Thylaeodus) indentatus	*	ec	s
Tripsycha (Tripsycha) tripsycha	*	ec	s
T. (Eualetes) centiquadra	*	ec	s
Dendropoma lituella	*	ec	s
Cerithium (Thericium)			
stercusmuscarum	*	em	h
Cerithidea mazatlanica	*	em	d
Epitonium (Nitidiscala) hindsii	*	em	c
E. (N.) barbarinum	*	em	c
Alora gouldii	*	em	?
Hipponix panamensis	*	em	h?
H. pilosus	*	em	h?
Calyptraea (C.) mamillaris	*	e	s
Crepidula excavata	*	e	s
C. incurva	*	e	s
C. lessonii	*	e	s

C. onyx	*	e	s
C. rostrata	*	e	s
C. striolata	*	e	s
C. uncata	*	e	s
Crucibulum (C.) ignarium	*	e	s
C. (C.) scutellatum	*	e	s
C. (C.) spinosum	*	e	s
C. (Dispotaea) concameratum	*	e	s
C. (D.) serratum	*	e	s
Natica (Natica) chemnitzii	*	im	c
Polinices (Polinices) uber	*	im	c
Neverita (Glossaulax) reclusiana	*	im	c
Cymatium (Turritriton) gibbosum	*	em	c
Solenosteira macrospira	*	em	c
Phos (Cymatophos) fusoides	*	em	c
P. (C.) dejanira	*	em	c
Columbella strombiformis	*	em	d
Anachis (Costoanachis) adelinae	*	em	d
A. (C.) nigricans	*	em	d
A. (?C.) sanfelipensis	*	em	d
A. (C.) varia	*	em	d
Mitrella xenia	*	em	d
Parametaria dupontii	*	em	d
Strombina (Strombina) sp.	*	em	d
Melongena patula	*	em	c
Nassarius (Nassarius) guaymasensis	*	em	c
N. (N.) versicolor	*	em	c
N. (Phrontis) iodes	*	em	c
N. (P.) brunneostoma	*	em	c
N. (P.) tiarula	*	em	c
Fusinus sp.	*	em	c
Oliva (Oliva) incrassata	*	im	c
O. (O.) spicata	*	im	c/o
Agaronia testacea	*	im	c
Olivella (Olivella) dama	*	im	c
Conus (Leptoconus) regularis	*	em	c
C. (L.) scalaris	*	em	c
C. (Ximeniconus) perplexus	*	em	c
Terebra armillata	*	im	c
T. elata	*	im	c
Agladrillia pudica	*	em	c
Crassispira (Striospira) kluthi	*	em	c
Pilsbryspira (P.) garciacubasi	*	em	c
P. (Nymphispira) bacchia	*	em	c
Pyramidella (Longchaenus) mazatlanica	*	em	c
Bulla (Bulla) gouldiana	*	im	c
Acteocina inculta	*	im	c
Melampus (Melampus) mousleyi	*	em	h
Pedipes unisculcatus	*	em	o

SCAPHOPODA

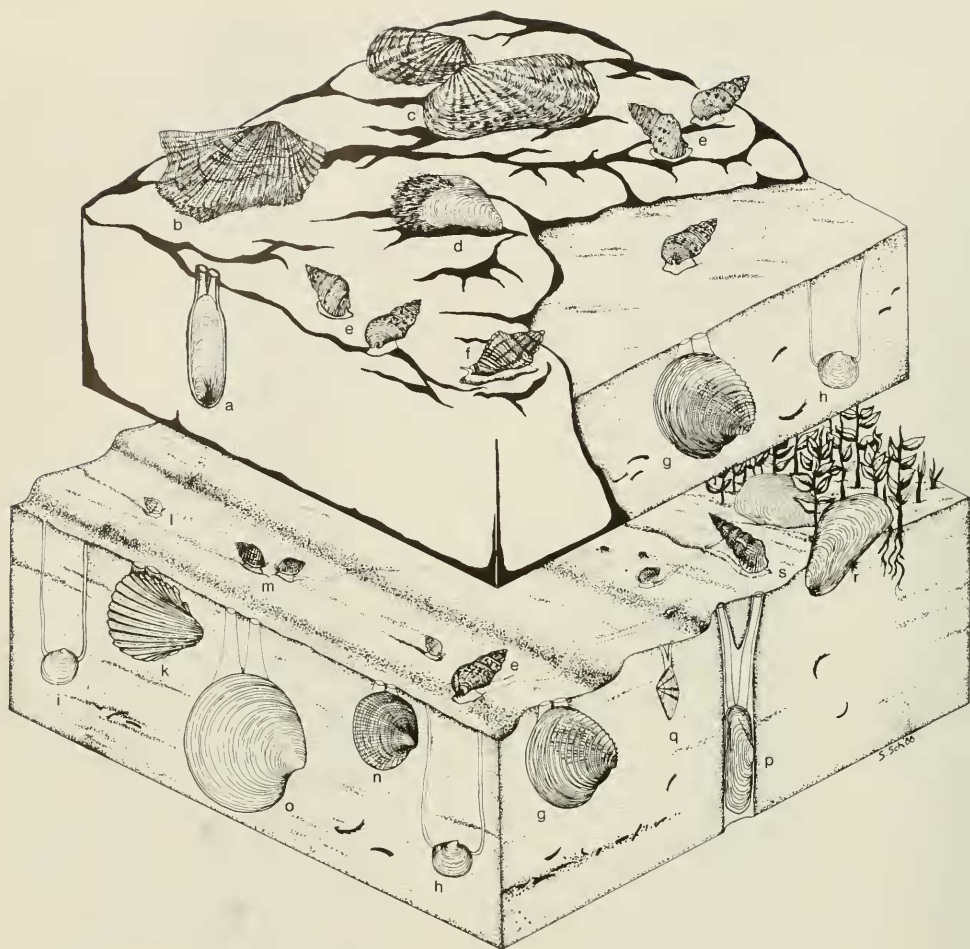|			
Tesseracme quadrangulare	*	is	d
Graptacme semipolitum	*	is	d
Laevidentalium splendidum	*	is	d

Fig. 10: Mode of life of some characteristic molluscs of rocky and sandy outer areas (upper diagram) and sandy mid flat areas to inner flat firmgrounds and salt marsh (lower diagram). a: *Lithophaga (Labis) attenuata*; b: *Arca (Arca) mutabilis*; c: *Cardita (Byssomera) affinis*; d: *Modiolus capax*; e: *Cerithium (Thericium) stercusmuscarum*; f: *Solenostetra macrospira*; g: *Chione (Chione) californiensis*; h: *Lucina (Callucina) lampra*; i: *Felaniella (Zemysia) sericata*; k: *Trachycardium (Mexicardia) panamense*; l: *Nassarius (Phrontis) iodes*; m: *Nassarius (Phrontis) brunneostoma*; n: *Protothaca (Tropithaca) grata*; o: *Dosinia ponderosa*; p: *Tagelus (Tagelus) affinis*; q: *Donax gracilis*; r: *Mytella guyanensis*; s: *Cerithidea mazatlanica*.

GENERAL DISTRIBUTION PATTERNS

This section describes some general distribution patterns of Bahia la Choya molluscan assemblages. We consider variations in shell density, species diversity, and the bivalve-gastropod ratio of taphocoenoses across the tidal flat.

Fig. 11 illustrates the variation in s h e l l d e n s i t y across the four transects. Shell density is given in weight of more or less complete shells and shell fragments per sampling unit (a bukket with a volume of 9 liters). Highest shell densities are recorded in outermost intertidal areas. As in these areas the sediment blanketing the underlying Pleistocene rock is very thin, concentration of shell material by winnowing appears likely. It can be explained by the higher energy level (breaker zone) at the seaward edge of the tidal zone. High shell densities are also found in the tidal channel of Transect B due to both a higher energy level and the input of shells from the spit (see above). The latter is responsible for the high shell
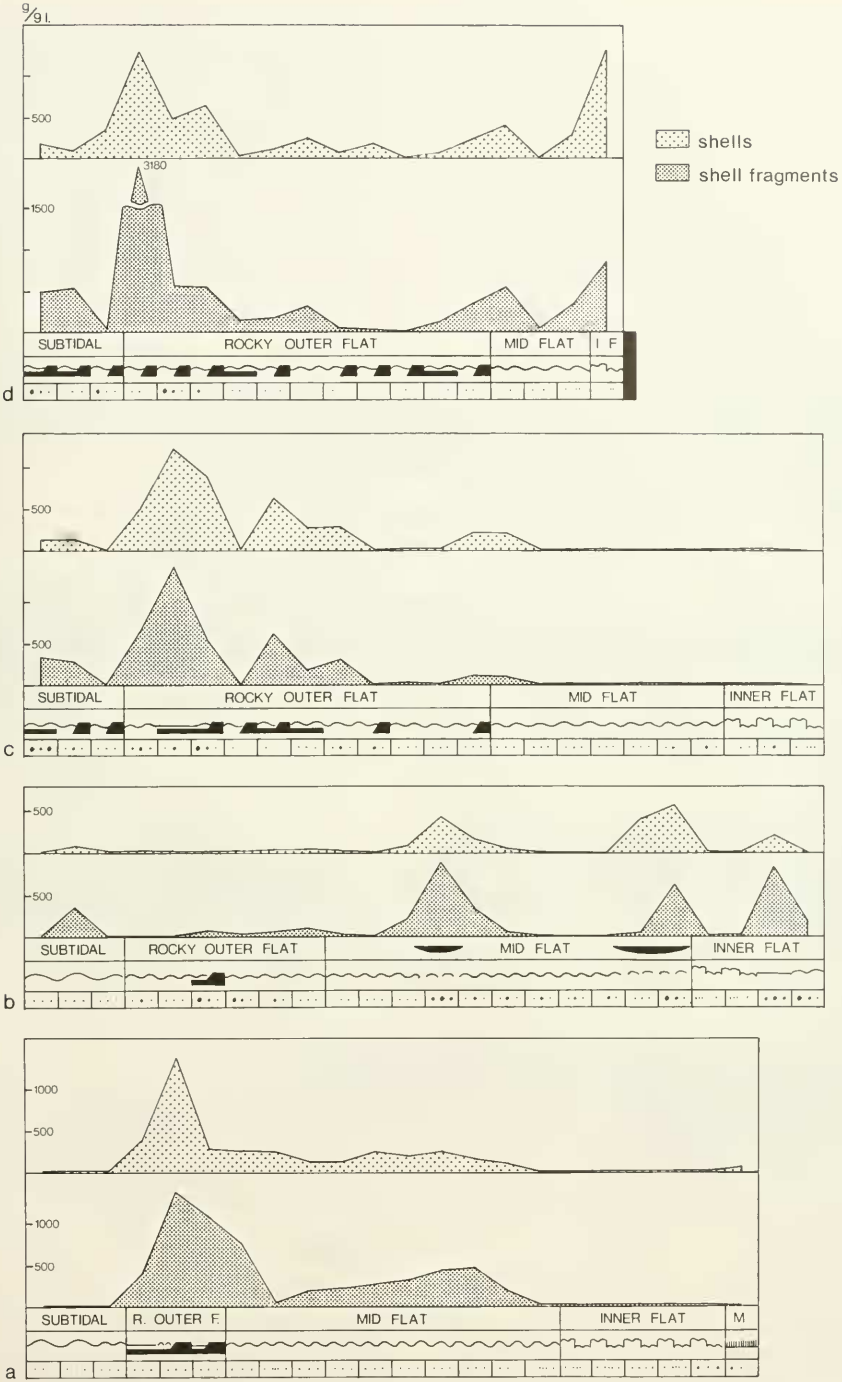
Fig. 11:   Variation in shell density across the four transects in gram per 9 liters of sediment. a—d: Transects A—D. For key see Fig. 12.

density close to shore in Transect B. The somewhat higher shell densities in Transects C and D are again related to a thin sediment cover indicative of low net rates of sedimentation caused by higher energy levels in the less protected northern part of the bay. Low shell density is characteristic of inner flat firmgrounds and can be explained by the lower burial potential of epifaunal species on such firm substrates.

The ratio between complete shells and shell fragments remains fairly constant across the flat, with fragments usually being more abundant.

Among the molluscs, scaphopods are very rare and invariably represent less than 0,5 % in terms of relative abundance.

They have therefore been neglected in the following discussion. Fig. 12 shows the bivalve-gastropod ratio along the four transects. Bivalves dominate numerically, often representing between 80 and 90 % of the molluscs except in inner flat areas (Transect A) and in the channel (Transect B). They are less dominant in hard substrate areas where they constitute 40−70 % of the fauna. This distribution pattern is closely related to the dominant life habits within both groups: For example, inner flat firmgrounds are largely colonized by epifaunal mobile gastropods, whilst on sandy substrates infaunal suspension-feeding bivalves dominate (see also FÜRSICH & SCHÖDLBAUER, this volume).
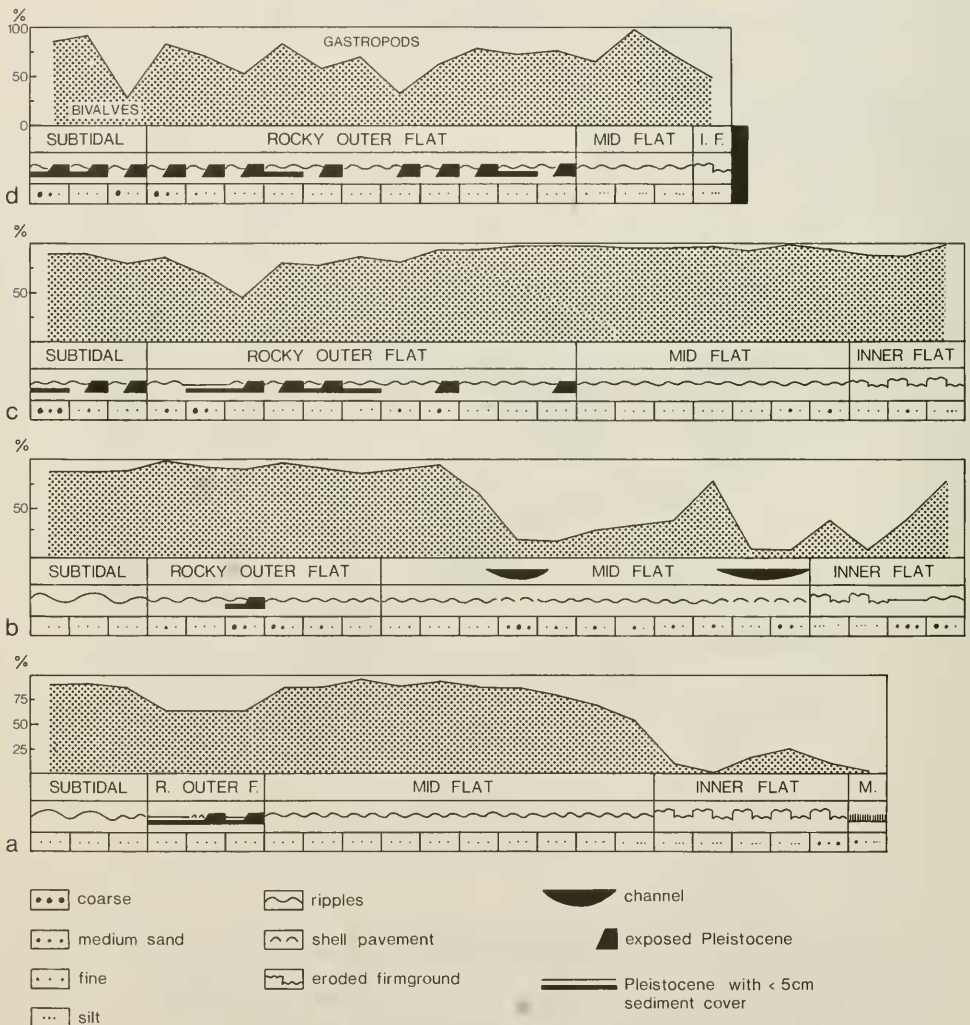
Fig. 12: Bivalve-gastropod ratio, expressed in numbers of individuals, along the four transects. a−d: Transects A−D.

Fig. 13 shows the diversity of bivalves and gastropods. Highest diversity values (expressed by the number of species) are found in outer to mid flat areas, whilst lowest values are encountered in the inner flat of Transects A and B. The low values recorded from the innermost subtidal station in all transects (most markedly in B, C, and D) can be partially explained by small sample sizes. The low diversity may also reflect the position of the breaker zone which restricts the number of species to those adapted to high turbulence levels.

In summary, these general distribution patterns suggest that the distribution of species across the tidal flat of Bahia la Choya is largely governed by ecologic factors and less by taphonomic processes such as post mortem transport.
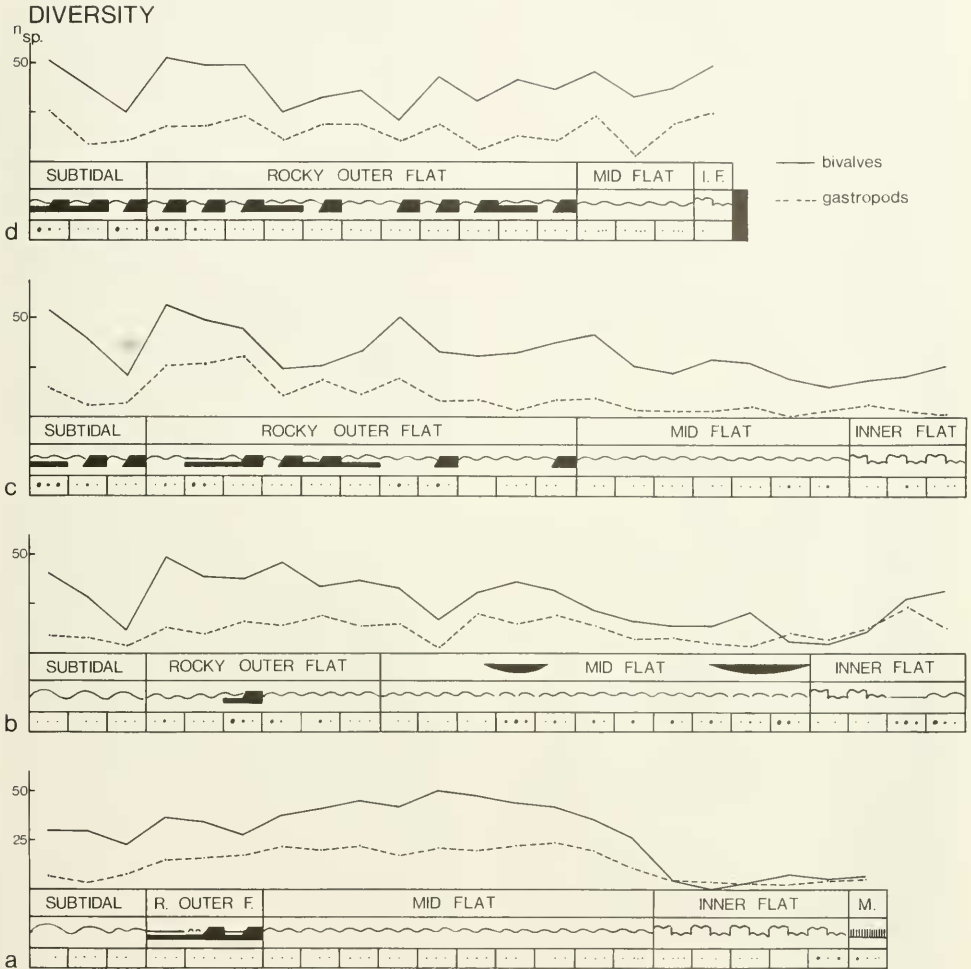
Fig. 13: Diversity (number of species) of bivalves and gastropods of the tidal flat taphocoenoses. a–d: Transects A–D. For key see Fig. 12.

ACKNOWLEDGEMENTS

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TAFELN

Plate 1

Fig. 1: Close-up view of pavement of shells and Pleistocene pebbles in trough of outer flat sand wave. Scale in cm.
Fig. 2: Exposed Pleistocene rocks covered with algae and numerous specimens of the gastropod *Cerithium*; outer flat.
Fig. 3: Outer flat sandwaves; wave crests 10 – 15 m apart.
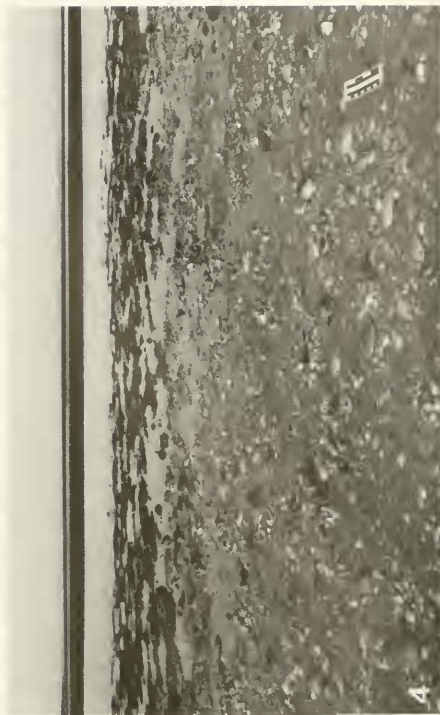Fig. 4: Shell pavement in trough of outer flat sandwave. Scale in cm.

Plate 1

Plate 2

Fig. 1: Scattered *Cerithidea mazatlanica* on inner flat firmground.
Fig. 2: Epifaunal *Cerithidea mazatlanica* and semi-infaunal *Mytella guyanensis* in salt marsh.
Fig. 3: Subrecent marsh assemblage consisting of chalky shells of articulated *Mytella guyanensis* in life position and *Cerithidea mazatlanica*.
Fig. 4: Coarse, gravelly substrate consisting of shells and reworked Pleistocene rocks at the bottom of the tidal channel; mid flat.

Plate 3

Plate 4

Biogenic sedimentary structures of the tidal flat.

Fig. 1: Cone of sediment produced by callianassid shrimp; outer flat. Scale in cm.
Fig. 2: Trace produced by the sea anemone *Calamactis;* mid flat.
Fig. 3: Ray pits on mid flat. Scale in cm.
Fig. 4: Burrow of *Tagelus* in inner flat firmground. Scale in cm.
Fig. 5: Trackway of hermit crab inhabiting *Cerithium* shell; mid flat.
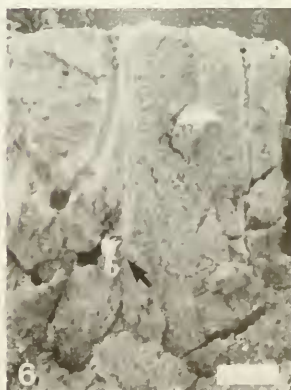Fig. 6: *Callianassa* burrows with producer (arrowed); inner flat. Scale: 1 cm.

Plate 5

Biogenic and physical sedimentary structures.

Fig. 1:   Crawling traces of the gastropod *Cerithidea mazatlanica* and *Nassarius brunneostoma;* inner flat.
Fig. 2:   Bank of tidal channel riddled with crab burrows; salt marsh.
Fig. 3:   Bubble sand near beach.
Fig. 4:   U-shaped ?amphipod burrow of inner flat firmground; scale in inches.
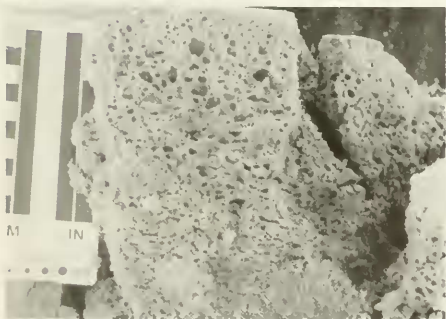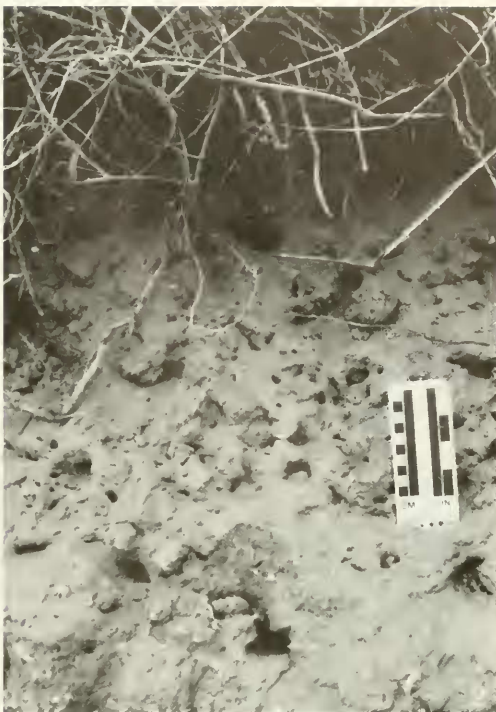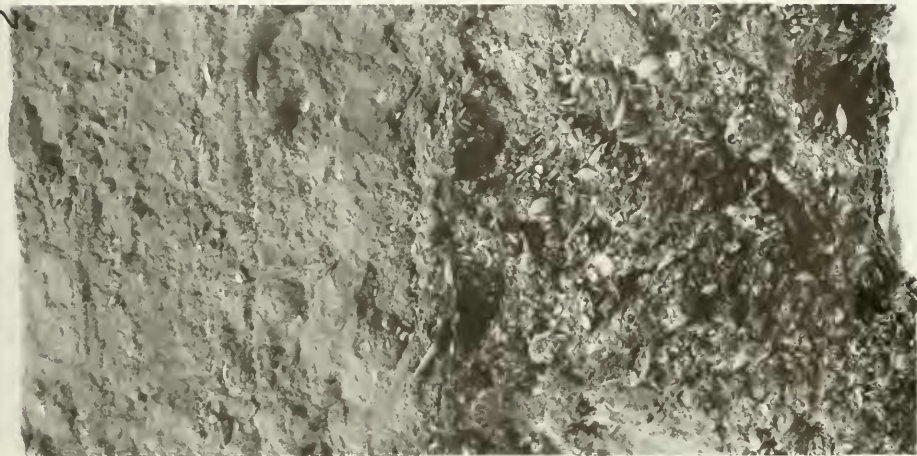Fig. 5:   Sand pellets near burrow opening of the fiddler crab *Uca.*

Plate 6

Resin casts of box cores; ×0.5.

Fig. 1: Bioturbated sediment from the crest of a sandwave; outer flat.
Fig. 2: Coarse shelly layer at base exhibiting a sharp boundary to the overlying laminated fine-grained sediment; inner flat.
Fig. 3: Heavily bioturbated and poorly sorted sediment of the salt marsh.

Plate 7

Fig. 1: Tidal creek eroding inner flat firmground; main tidal channel in background. Scale in cm.
Fig. 2: Salt marsh. Scale in cm.
Fig. 3: Tidal channel of the salt marsh at low tide.
Fig. 4: Mesita-like topography of the inner flat firmground. Scale in cm.

Plate 8

Fig. 1: Partially eroded *Tagelus* sp. in growth position. Tidal creek of inner flat.
Fig. 2: Entrance of crab burrow. Point bar of tidal channel, salt marsh.
Fig. 3: Current lineation in tidal channel; view from outer flat toward shore.
Fig. 4: Preferred orientation of bivalves *(Tagelus* sp.) and gastropods *(Cerithidea)* in the tidal channel of the mid flat. The long axis of shells is parallel to the ebb current (from left to right). Scale in cm.
Fig. 5: Biofabric of mollusc shells and shell debris of the spit. Resin cast of box core. Scale: 1 cm.

FÜRSICH, F. T., FLESSA, K. W., ABERHAN, M., FEIGE, A. and SCHÖDLBAUER, S.: Sedimentary habitats.

Plate 8

Plate 9

Characteristic bivalves of Bahia la Choya, deposited in Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, under the collection number BSP 1990 XI.

Fig. 1: *Felaniella (Zemysia) sericata* (REEVE) × 3. BSP 1990 XI 1.
Fig. 2: *Lucina (Callucina) lampra* (DALL); × 3. BSP 1990 XI 2.
Fig. 3: *Chione (Chione) californiensis* (BRODERIP); × 1. BSP 1990 XI 3.
Fig. 4: *Megapitaria squalida* (SOWERBY); × 1. BSP 1990 XI 4.
Fig. 5: *Tellina (Merisca) brevirostris* DESHAYES; × 3. BSP 1990 XI 5.
Fig. 6: *Parvilucina (Parvilucina) mazatlanica;* (CARPENTER); × 4.
Fig. 7: *Donax navicula* HANLEY; × 3. BSP 1990 XI 6.
Fig. 8: *Protothaca (Tropithaca) grata* (SAY); × 1. BSP 1990 XI 7.
Fig. 9: *Tagelus affinis* (C. B. ADAMS); × 1. BSP 1990 XI 8.
Fig. 10: *Trachycardium (Mexicardia) panamense* (SOWERBY); × 1. BSP 1990 XI 9.
Fig. 11: *Laevicardium elenense* (SOWERBY); × 4. BSP 1990 XI 10.
Fig. 12: *Corbula marmorata* HINDS; × 4. BSP 1990 XI 11.
Fig. 13: *Dosinia ponderosa* (GRAY); × 1. BSP 1990 XI 12.

Plate 10

Characteristic bivalves and gastropods of Bahia la Choya, deposited in the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, under the collection number BSP 1990 XI.

Fig. 1: *Cardita affinis* SOWERBY; × 1. BSP 1990 XI 13.
Fig. 2: *Arca (Arca) pacifica* (SOWERBY); × 1. BSP 1990 XI 14.
Fig. 3: *Modiolus capax* (CONRAD); × 1. BSP 1990 XI 15.
Fig. 4: *Pteria sterna* (GOULD); × 1. BSP 1990 XI 16.
Fig. 5: *Olivella (Olivella) dama* (WOOD ex MAWE, MS); × 3. BSP 1990 XI 17.
Fig. 6: *Cerithium (Thericium) stercusmuscarum* VALENCIENNES; × 2. BSP 1990 XI 18.
Fig. 7: *Crepidula excavata* (BRODERIP); × 2. BSP 1990 XI 19.
Fig. 8: *Agaronia testacea* (LAMARCK); × 1.5. BSP 1990 XI 20.
Fig. 9: *Theodoxus (Vittoclithon) luteofasciatus* MILLER; × 4. BSP 1990 XI 21.
Fig. 10: *Crucibulum (Crucibulum) spinosum* (SOWERBY); × 1. BSP 1990 XI 22.
Fig. 11: *Solenosteira macrospira* BERRY; × 1. BSP 1990 XI 23.
Fig. 12: *Cerithidea mazatlanica* CARPENTER; × 2. BSP 1990 XI 24.
Fig. 13: *Nassarius (Phrontis) iodes* (DALL); × 4. BSP 1990 XI 25.
Fig. 14: *Nassarius (Phrontis) brunneostoma* (STEARNS); × 4. BSP 1990 XI 26.